IMMEDIATE RESPONSES OF WILD BEE COMMUNITIES TO A LARGE-SCALE BURN IN SAVANNAH HABITAT

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A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTERS OF SCIENCE

GRADUATE PROGRAM IN BIOLOGY
YORK UNIVERSITY
TORONTO, ONTARIO

MAY 2013

Abstract

Little is known about the effects of large-scale fires on essential pollinators, such as bees. A large wildfire occurred in the savannahs of Mburucuyá National Park, Argentina, providing one year of both pre- and post-burn data. This allowed for an impact assessment of distance from fire edge using species diversity and guild characterization, based on nesting materials and body size, to examine bee community responses to fire. Our results generally agree with those of earlier smaller-scale fire impact studies upon bee communities: immediate declines in species richness and abundance but increases in diversity post-burn as well as similar responses from bee guilds based on nesting requirements. Our study suggests: (1) above-ground nesters are unable to colonize recently burned habitat as quickly as ground-nesters regardless of survival rates *in situ*, (2) ground-nesting bees, regardless of size, are least affected by distance from foraging or nesting resources, (3) patterns of fire impacts on bees become exacerbated near the middle of a large burn area, and (4) large-scale fires will have a greater impact upon above-ground nesters than do smaller-scale burns.

Dedication

I dedicate this thesis to my mother, Griselda Veiga, who has always been a pillar of strength and a driving force in my life. I would also like to dedicate this work to my father, Jorge Veiga, and my step-father, Roy Crocker, who were both proud supporters of my continued education from the very beginning but who were unable to see it through to completion. You are both sorely missed.

Acknowledgements

This work was made possible by many individuals to whom I am extremely grateful. I would like to start by expressing my deepest gratitude to my supervisor and mentor, Dr. Laurence Packer, for providing this amazing opportunity and encouraging me to embark on this project. His guidance, advice, and continued support throughout this endeavor have made this experience grand. I would also like to thank him for sparking my initial interest in bees as an undergraduate and for opening my eyes to world of entomology. In the future, I look forward to expanding my education in this field using the knowledge acquired throughout my studies with Dr. Packer.

I would like to thank my Packer Lab peers at York University, especially Alana Taylor-Pindar, who have offered their friendship and knowledge throughout various challenges during this study. I cherish the many great experiences we have shared over the years.

This work would not have been possible without the help and generosity from members of Mburucuyá National Park for the Northeastern parks of Argentina (NEA). I would particularly like to thank Paula Cichero, Director of the NEA, for allowing this collaboration, Lorena Paszko for her continued support and hospitality, and park staff at Mburucuyá National Park for trap maintenance and care. I would also like to thank Dr. Pablo Tubaro, Dr. Arturo Roig-Alsina, and colleagues at the Museo Argentino de

Ciencias Naturales (MACN) in Buenos Aires for facilitating specimen transportation, identification and lab space.

Special thanks to my family in Canada for their continued support and encouragement as well as my family in Argentina who lived with "boxes of bugs" in their spare rooms and had their kitchens remodeled into species identification and pinning stations.

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1.0 Introduction

Large, uncontrolled fires remain difficult to manage, incur high economic costs and usually endanger human safety. They are easily depicted by others as a destructive phenomenon (Bowman *et al.*, 2009; Bowman *et al.*, 2011; Dube, 2007; Moreira *et al.*, 2011; Pyne, 1994). In recent years, fire studies have shown burns to often be a positive ecological force by enhancing flowering, seed germination, seedling recruitment, reducing understory litter, preparing seed beds, and increasing biodiversity (Burton *et al.*, 2011; Campbell *et al.,* 2007; Kimura and Tsuyuzaki, 2011; Potts *et al.*, 2001; Thompson *et al.,* 2006). In conservation and restoration efforts, fire is often used as a tool to limit the spread of invasive, non-native species (Brooks *et al.*, 2004; Campbell *et al.*, 2008; Emery *et al.,* 2011; Hall *et al.*, 2012; Valentine and Schwarzkopf, 2009) and to return a habitat to an earlier successional stage (Force, 1981; Joubert *et al.*, 2012; Slik *et al.*, 2011). Various organisms show adaptations to the effects of fire disturbance, whether they are under constant threat in fire-prone (fire-dependent) environments or not (fire-independent) (Burton *et al.*, 2011; Force, 1981; Whelan, 1995). An important component of fire ecology studies is how different populations or communities respond to fire disturbance events (Anderson *et al.*, 1989; Biganzoli *et al.*, 2009; Campbell *et al.*, 2007; Haney *et al.*, 2008; Potts *et al.*, 2003a; Tasker *et al.*, 2011).

Understanding the essential role of pollinators within an environment may be one of the keys to effective community restoration and maintenance of ecosystem function (Biesmeijer *et al.*, 2006; Breeze *et al.*, 2011; Dixon, 2009; Fishman and Hadany, 2010;

Pauw, 2007; Winfree *et al.*, 2007), especially after an ecological disturbance such as a fire (Campbell *et al*,. 2007; Potts *et al.*, 2001; 2006; Taylor and Catling, 2011). Pollination by insects in various habitats is a vital process that should be conserved since pollinators help maintain a diversity of plants and aid in crop pollination (Carvalheiro *et al.*, 2010; Fliszkiewicz *et al.*, 2011; Greenleaf and Kremen, 2006; Klein *et al.*, 2003; Ricketts, 2004). Bees (Hymenoptera: Apoidea) are among the most important pollinators of angiosperms and are found on every continent with the exception of Antarctica (Michener, 2007). There are close to 20 000 described bee species (Packer, 2010; The Polistes Corporation, 2013) and they comprise the vast majority of pollinating insects (Ollerton *et al.*, 2011) with their pollinating services valued at approximately $200 billion per year (Gallai *et al.* 2009). Approximately 85% of all flowering plants depend on animals for pollination (Ollerton *et al.,* 2011) with an estimated 75% of crop species and 35% of crop value accredited to pollination by animals (Klein *et al.*, 2007; Dixon, 2009).

The functional importance of bees within most ecosystems is reflected by their pollination services since the reproduction of most terrestrial plant species relies on the process of pollination (Ollerton *et al.*, 2011). In this way, bees help maintain plant diversity along with the diversity of flower-dependent organisms such as themselves (Potts *et al.*, 2006). However, humans have been the cause of a variety of environmental disturbances for bees including habitat fragmentation, climate change, pathogen spillover, land use changes, planting of extensive monocultures, and introduction of exotic species to name a few (Badano and Vergara, 2011; Colla *et al.*, 2006; Holzschuh *et al.*, 2011;

Otterstatter and Thomson, 2008; Pauw, 2007; Tilman and Lehman, 2001). Unsurprisingly, native bee populations have shown declines in abundance and range (Biejsmeier *et al.*, 2006; Burkle *et al.*, 2013; Colla and Packer, 2008; Grixti *et al.*, 2009; Steffan-Dewenter *et al.*, 2005; Williams and Osborne, 2009) making understanding bee community composition of the utmost importance. Due to their direct dependence on the flora and abiotic factors within their habitats, bees have become important biological indicators for the state of the environments they inhabit (Fishman and Hadany, 2010; Kerr *et al.*, 2000; Potts *et al.*, 2001; Tscharntke *et al.*, 1998; Williams *et al.*, 2010). Indicator taxa are selected based on their ability to reflect changes caused by an environmental stressor on the selected taxa as well as other organisms within a given ecosystem (Kerr *et al.* 2000). Stressors affect bee guilds differently (Grixti and Packer, 2006; Sheffield *et al.* 2013; Williams et al., 2010); furthermore, the production of sterile diploid males makes bees particularly prone to the effects of small population size and more sensitive to environmental changes (Packer *et al.*, 2005; Zayed and Packer, 2005). These factors establish bees as model organisms for environmental health and diversity studies (Packer, 2010; Williams and Osborne, 2009).

Bees are dependent on floral communities as well as nesting resource availability, and disturbances, such as fire, affecting those resources will also affect bee communities. Habitat changes due to grazing, and fragmentation are known to affect bee community structure (Aizen and Feinsinger, 1994; Murry *et al.* 2012; Sjodin *et al.*, 2008; Vulliamy *et al.*, 2006). Some studies have explored the effect of fire, fire attributes, and other

disturbances on essential pollinators such as bees (Campbell *et al.,* 2007; Moretti *et al.,* 2009; Potts *et al.,* 2001; 2003a; 2003b; 2005; Taylor, 2007; earlier work reviewed by Williams *et al.,* 2010). In general, the latter studies have been comparisons of burned and unburned sites or re-visitations of a burned site at differing post-burn ages. A study by Potts *et al.* (2003a) showed instantaneous responses to fire where bee communities drastically declined immediately post-burn followed by a rapid recovery, with diversity peaking within the first 2 years post-burn and steadily declining thereafter. Other studies inferred long-term fire effects on pollinator communities using various time-since-burn plot ages (Potts *et al.*, 2005; Moretti *et al.,* 2009). In general, most bee studies have monitored community responses to an environmental disturbance by analyzing diversity in terms of species richness and abundance (Potts *et al.*, 2001; 2003a; 2003b). However, these changes in community composition can sometimes be distorted by undetected environmental conditions (Magurran, 2004). Therefore, understanding how environmental conditions affect the species composition of a whole community becomes important. Floral and nesting resource availability, species diversity, and guild characterization have been used to explain changes in bee community structure (Moretti *et al.,* 2009; Potts *et al.*, 2003b; 2005; Williams *et al.,* 2010). Though guild characterization of species does not examine individual species responses to a disturbance, this method of analysis (based on traits such as required nesting resources and body size) allows for pooling of species with broadly similar habitat requirements to

make generalized conclusions about community composition as a whole (Grixti and Packer, 2006; Potts *et al.*, 2005; Williams *et al.*, 2010).

Previous fire studies on bees have been limited to the northern hemisphere and focused on small-scale burns, ranging from 0.01km² (1ha) (Moretti *et al.* 2009; Potts *et al.*, 2003a; 2003b; 2005; 2006) to 0.1km² (10ha) (Campbell *et al.*, 2007). In general, maximal flight distances positively correlate to body size (Araujo *et al.*, 2004; Cane, 1987; Greenleaf *et al.*, 2007; Osborne *et al.*, 2008). Larger bees, such as bumble bees, have been known to forage up to 1.5km (Osborne *et al.*, 2008) and honey bees can forage anywhere between 50m to over 5km (Hagler *et al.*, 2011) while, smaller species may be restricted to foraging within an area of only 50m² (Cane *et al.*, 2006). Most bees have recorded foraging distances within a 2km radius (Rands and Whitney, 2011) with a majority of solitary bees foraging under a 1km radius from their nests (Gathmann and Tscharntke, 2002; Zurbuchen *et al.*, 2010). Given that many bees seem capable of foraging over distances approaching 1km, previous burn study sites can be considered small-scale, making it unclear whether bees found in the centre of a previously burned area survived the burn or were collected while foraging from nests outside of the affected area.

The study examined the effect of a wildfire that was considered to be large-scale when taking into account bee foraging ranges. The wildfire consisted of four events which occurred consecutively between September and October of 2009 and, in combination, consumed most of the savannah habitat within the park. This study

specifically examined the effect of the fourth and final large-scale fire, which consumed approximately 14.2km² within the southern half of the park (sectioned off in Figure 1), on a community of wild bees using samples from malaise traps set within Mburucuyá National Park, Corrientes, Argentina. Two years of data were collected from April-October of 2009 (pre-burn data) and 2010 (post-burn data) with traps spanning an area approximately 4km². This unique opportunity enables us to be the first to test differential responses of bee functional guilds to fire based on increasing distance from the edge of a very large burn.

Ground-nesting bees are known to dominate savannah and grassland habitats (Michener, 2007) and are those most likely to survive a wildfire (Cane and Neff, 2011). Meanwhile, bee body size is correlated with foraging distance (Araujo *et al.,* 2004; Cane, 1987; Greenleaf *et al.,* 2007; Osborne, 2008) and may influence how bees are able to recolonize a recently burned area. In general, larger bees are able to travel greater distances than smaller ones for food and nesting resources, making them capable of recovering more rapidly from disturbances. We expect bee communities deep within the burned area to be those most directly affected by the recent burn since most bees are limited in foraging range.

The objectives of this study are to determine the effects of a large-scale burn on wild bee communities in palm savannahs of north-eastern Argentina by examining the following hypotheses:

H1: There is a significant impact upon bee community composition resulting from a large-scale burn.

H2: Ground-nesting bees will be less impacted by a recent large-scale burn than above-ground nesters because soil effectively insulates against high temperatures whereas above-ground nesting bees' nest sites are destroyed.

H3: The proportional abundance of ground-nesting bees will be positively correlated with distance from unburned habitat because they will have survived *in situ* whereas above-ground nesting bees will have to recolonize from outside the burned area.

H4: Distance from an unburned edge will have less of an effect on larger bees because of their greater vagility.

2.0 Methods

2.1 Study Site

Bees were collected from Mburucuyá National Park (28°1.102'S, 58°1.699'W) (henceforth MNP), located in the north-eastern region of Argentina in the province of Corrientes (Figure 1). The following description of ecological conditions in MNP comes from a series of reports (Heinonen, 2001; Parque Nacional Mburucuyá, 2004a; 2004b; 2004c; 2004d; 2005a; 2005b; 2006; 2007a; 2007b; 2008a; 2008b; Paszko, 2007; 2009), personal observations and communication with park staff. The park is within the Neotropical grassland and savannah ecoregion (Sarmiento, 1984) and encompasses 177km^2 of land, dominated by short and tall grassland. Though much of the lower elevation areas of the park are covered in wetland marsh, most of the total area is representative of the typical Yatay (palm) savannahs of north-eastern Argentina (Figure 2). The dominant plants are *Andropogon lateralis* (Poaceae) and *Paspalum notatum* (Poaceae), with *Butia yatay* palms (Arecaceae) grouped or scattered, typically on level plains, and patches of forested areas that form relatively small, dense clusters scattered throughout the higher elevation regions within the park. The park is bisected by a single dirt road which is impassable after rain limiting access to the park. One information area, one campsite and two recreational pathways exist within the park, leaving the vast majority of it untouched by tourism.

The subtropical climate with extended dry periods make the savannah region of Argentina prone to wildfires, especially at winter's end when weather is characterized by heavy winds and little rainfall (Heinonen, 2001; Paszko, 2007, 2009; Pelaez *et al.,* 2003). In South American Neotropical savannahs, these conditions are typically found between August and November (Heinonen, 2001; Paszko, 2007; 2009; Sarmiento, 1984). Controlled burns in areas prone to fire have been shown to maximize biodiversity when mosaics of different fire regimes have been applied (Bond and Parr, 2010), promoting a variety of conditions that hinder single-species dominance for both flora and fauna in Argentina (Feldman and Lewis, 2005; Kunst *et al.*, 2003; Rostango *et al.*, 2006) and worldwide (Brooks *et al.,* 2004; Campbell *et al.,* 2007; Kimura and Tsuyuzaki, 2011; Potts *et al.,* 2003a; Pyke *et al.,* 2010). As such, an attempt at bi-annual controlled burns for various areas within the park was introduced in 1996 with the objective of preventing the area from undergoing succession to forest and maintaining MNP as natural grassland and savannah. MNP staff generally burn their various savannah patches every 2-6 years depending on biomass accumulation and yearly precipitation, though historically the savannahs burned more frequently.

Prescribed burns had been arranged for several areas within the park for 2008 and 2009, however, low annual precipitation and varying weather conditions hindered proceeding with plans (Paszko, 2009). Nevertheless, a combination of four large consecutive wildfires occurred in the early spring period of 2009 between September and October consuming much of the park. The fourth and final fire of 2009 consumed most

of the savannah habitat south of the road that bisects the park (approximately 14.2km^2), including our study site.

2.2 Bee Sampling

Bee sampling took place between April and October in 2009 and 2010: seven standard Townes style, fine mesh Malaise traps (see below; Sante Traps Ltd., Lexington, KY) were set along a transect spanning approximately 4km within savannah habitat scheduled for a small controlled burn (Table 1, Figure 1). This area had remained unburned for at least two years prior to the study (Table 1) and was chosen in order to avoid pseudo-replication of trap sites by selecting areas with similar fire regimes and burn history (Potts *et al.,* 2001; 2003b; Moretti *et al.,* 2009). However, in late October 2009, a large wildfire burned the entire study area as well as most of the surrounding habitat. This permitted us to assess the impact of distance from burn edges on the native bee community. Patterns were not as clear cut as they might have been because the fire was accidental and our trap locations were selected based on an expected smaller burn area that would have been planned and controlled. Of the original seven traps, only five new traps were available for use post-burn. Thus, only the same five traps sites from 2009 and 2010 were used to compare data between years; providing one year of pre-burn data and one year of post-burn data (Figure 1). Trap coordinates and distances between traps and fire edges were obtained using a Garmin eTrex Vista handheld GPS unit with general

accuracy between 3-5m. All traps were placed in savannah habitat within MNP. Trap 1 and 2 were in open, tall-grass savannah with dispersed palm trees and dominated by tall grasses (Figure 2) while traps 3, 4, and 5 were in areas more similar to one another in savannah habitat containing a greater density of palm trees and shrubs (Figure 3).

Malaise traps are a passive form of sampling that work by intercepting flying insects moving from one location to another (Bartholomew and Prowell, 2005; Fraser *et al.,* 2007). Several studies within savannah habitat and fire studies on pollinating insects worldwide have shown Malaise traps to be efficient in the capture of diverse insects, especially aculeate Hymenoptera species (Campbell and Hanula, 2007; Darling and Packer, 1988; Kerr *et al.,* 2000; Sackmann, 2006; Sugar *et al.,* 2001). While use of multiple sampling techniques, such as pan traps, have been shown to increase sampled diversity (Westphal *et al.,* 2008), a combination of pan collections and Malaise traps over such a large area with limited time and resources between collection dates was unfeasible. Each trap was positioned at right angles to adjacent denser vegetation (Gressit and Gressit, 1962) oriented north-south so that the collecting head faced in the direction that would receive the most sunlight throughout the day (Noyes, 1989). Trap collecting heads were filled with 96% ethanol and checked bi-weekly, or on the next weather permitting day. New Malaise traps were used at the beginning of each year in April to maximize collection efficiency and to avoid biases that might arise through trap material fading due to prolonged exposure to intense sunlight (Pinto Durante *et al.,* 2010).

2.3 Bee Identification

All bees collected were identified to genus following Michener (2007) and to species using various taxonomic keys (Table 2). Experts verified identifications as follows: Dr. Arturo Roig-Alsina, Natural Sciences Museum of Argentina (MACN), Buenos Aires, Argentina for most Apidae; Rocio Gonzalez-Vaquero, MACN, for most *Pseudagapostemon*; Milagros Dalmazzo, MACN, for most *Augochlora*; Dr. Terry Griswold, USDA, Bee Biology and Systematics Laboratory, Logan, Utah, USA for most Anthidiini; Dr. Cory Sheffield, Royal Saskatchewan Museum, Regina, Canada for most other Megachilidae; and Dr. Jason Gibbs, Cornell University, New York, USA for most *Lassioglossum (Dialictus)*. Specimens for which species-level identification became difficult due to lack of keys were sorted into morphospecies based on distinct morphological characteristics and subsamples of all species were submitted to the University of Guelph for DNA barcoding (see below). All specimens from this study will be housed at MACN, except for voucher specimens that are retained at the Packer Collection York University (PCYU), Toronto, Canada.

DNA was extracted from a single leg for sequencing of the barcode region of cytochrome *c* oxidase subunit 1 (Herbert *et al.*, 2003a; 2003b); all specimen information is available on the barcode of life data system BOLD (www.boldsystems.org). DNA was extracted from each sample via automated extraction protocols for 96-well plates (Ivanova *et al.*, 2006) and amplified using a single set of primer pairs (Hebert *et al.*, 2003a). Sequencing was performed at the Canadian Centre of DNA Barcoding (CCDB)

Biodiversity Institute of Ontario at the University of Guelph following standard polymerase chain reaction (PCR) and sequencing reaction protocols (Hajibabaei *et al.*, 2005), available at www.ccdb.ca/pa/ge/research/protocols.

2.4 Guild Classification

Pooling bee species based on guild characteristics allows for a better overall assessment of disturbance effects upon a whole community (Grixti and Packer, 2006; Potts *et al.*, 2003b; 2005; Williams *et al.*, 2010). Bees can be partitioned into several exclusive guilds based on their nesting habits, even in the absence of species level identification, since closely related species tend to share nesting characteristics (Michener, 2007; Raw, 2007). Guilds used in the past have included a generalized division of species based on various nesting resource requirements (Potts *et al.*, 2005), a less finely divided approach using above and below-ground nesting (Williams *et al.*, 2010), dietary breadth, sociality and body size (Potts *et al.*, 2003b; Williams *et al.*, 2010) (Table 2). However, the data were certain for a large enough proportion of the taxa to include nesting resource and body size only.

Nesting guild classification was performed following Potts *et al.* (2005) and Williams *et al.* (2010). A total of five nesting guilds were used to sort bee communities: ground-nesters, stem-nesters, wood-nesters, cavity-nesters and cleptoparasites. Ground nesters (mining bees) make their nests in soil at varying depths and are generally most

abundant and dominant in open habitat areas. Stem-nesters generally construct their nests using pre-existing, relatively small cavities; usually in pithy or hollow plant stems, abandoned insect burrows, or small cavities between rocks or bricks. Wood nesters bore holes into wood or use holes already in existence in woody substrates to build their nests. Cavity nesters are social bees that use larger, pre-existing cavities or build hives. Among the bees we obtained, only feral *Apis mellifera* (Linnaeus) was classified as a cavity nester and considered to nest above-ground for the purpose of this study. Lastly, cleptoparasitic bees parasitize nests of other bee species and therefore rely on nests of other bees. Since few cleptoparasitic specimens were sampled overall and the species they parasitized were generally unknown, cleptoparasites were removed from guild analyses.

Body size is easily measured for all species. In general, larger bees are able to fly greater distances than smaller ones (Araujo *et al.,* 2004; Cane, 1987; Greenleaf *et al.,* 2007; Osborne, 2008), making them less susceptible to larger scale habitat disturbances such as fire. Following Cane (1987), bee body size was established by measuring the distance between wing bases, intertegular (IT) distances, as a broad indicator of dry body mass. Due to possible species size discrepancies between sexes, 5-10 female individuals, wherever possible, were measured using a dissecting microscope and calibrated ocular micrometer to calculate mean IT distance and standard deviation. The same number of males was used if insufficient female specimens had been collected. Three distinct categories of body size were used: small (<1.24mm), medium (1.24mm-2.23mm), and

large (>2.23mm) (Table 2). Discrepancies where species mean body sizes landed directly on the divisor line were excluded from data analyses requiring body size.

2.5 Statistical Analysis

Chi square tests were used to determine differences in number of specimens and species richness and guild composition between years using Minitab 16 (Minitab Inc., 2010). Shannon diversity and evenness measures were tested using t-test statistics following Magurran (1988). Single linkage Jaccard and Bray-Curtis similarity indices were analyzed via clustering dendrograms using Community Analysis Package 3.2 (Henderson and Seaby, 2004). Ordination was used to identify general bee community associations with respect to presence and absence of a fire disturbance. Following Potts *et al.* (2005; 2006), Canoco 4.5 (Lepš and Šmilauer, 2003) was used to generate PCA diagrams in order to visualize patterns among all species and traps (Krebs, 1999). Specimen samples from each trap were plotted together without differential weighting of any species or samples in order to determine how community composition differed between burned and unburned years. Effects of distance from unburned habitat on proportional abundance and guild composition were determined using comparison of linear regression slopes (Zar, 1999) of pre- and post-burn data using SPSS 20 (IBM SPSS Inc., Chicago, IL, USA).

3.0 Results

A total of 771 individual bee specimens were collected representing 23 genera and 64 species (Table 2). A total of 547 specimens were collected in 2009 from 20 genera and 56 species and 224 specimens from 19 genera and 37 species in 2010.

All diversity indices showed significant differences between 2009 and 2010 (Table 3). Number of specimens and species richness decreased by 41% ($p<0.001$) and 66% ($p=0.023$), respectively, from pre-burn to post-burn years. Meanwhile, Shannon diversity and evenness increased by 5% ($p<0.001$) and 17% ($p<0.001$), respectively.

Clustering analyses, both Jaccard and Bray-Curtis measures, showed complex patterns (Figure 4, 5). Both dendrograms indicate that samples clustered by year, with the exception of trap 2 in 2009 and trap 5 in 2010. This is because fewer bees overall were caught in 2010, but trap 2 caught the fewest in 2009 and trap 5 caught the most in 2010 thereby placing them among the alternate year's data (Table 4).

PCA plots for 2009 and 2010 are shown in Figures 6 and 7, respectively, illustrating bee community composition and trap sites within MNP for pre-and post-burn years. Pre-burn plots (eigenvalues: axis 1=0.880, axis 2=0.066) displayed greater species variation among traps 3, 4, and 5 with the majority of bees associating with trap 4 (Figure 6). Post-burn bee communities showed large differences in composition (eigenvalues: axis 1=0.956, axis 2=0.033) with most species abundance and variation associating with trap 5 (Figure 7). In both PCAs, the bees were less commonly sampled by traps 1 and 2.

PCA plot comparisons revealed a known environmental fire disturbance to have caused a shift in bee community composition whereby the majority of bee abundance and diversity was spread among 3 traps in 2009 to mainly a single trap location in 2010. In both cases, traps 1 and 2 clustered together and caught the fewest bees. These immediate shifts in trap composition between years may be indicative of similarities in habitat composition or disturbance attributes. Analyses by guild provide clearer explanations for these patterns.

The guilds showed a significant difference in relative abundance between collecting years ($p<0.001$; $X^2_{3,1}$) (Table 4). Due to small sample sizes, stem, wood, and cavity-nesting bees were grouped into a single above-ground guild for the duration of the study. The abundance of both above-ground and below–ground nesters decreased sharply post-burn. However, ground-nesting bees proportionally dominated in both years with 411 of 540 bees in 2009 and 173 of 217 bees in 2010, resulting in a 4% decrease in above-ground nesting bee proportional abundance post-burn.

Prior to a large-scale burn, ground-nesting bees occurred in similar proportions among traps and there was no significant relationship with the distance from the (future) burned edge ($p=0.307$; Figure 8) with only 33% of the data explained by the trendline. In contrast, the proportion of ground-nesters per trap increased markedly with distance from unburned edges after the burn ($p=0.002$) with 97% of the variation in post-burn data explained.

There was no significant pattern relating body size to distance from the unburned edge pre-burn (small bees, p=0.804; medium bees, p=0.479; large bees, p=0.215). However, post-burn, large-sized bees showed a significant change in proportional abundance (p=0.023) with respect to distance from unburned habitat (Figure 9), with fewer large bees nearer to the centre of the burn. Both small and medium-sized bees did not differ significantly in abundance with distance from the edge after the burn (p=0.949 and p=0.080, respectively).

Pre-burn data showed no significant patterns for nest site and body size combinations versus distance from the unburned edge (small ground nesters, p=0.845; medium ground nesters, p=0.443; medium above-ground nesters, p=0.329; large ground nesters, p=0.641; large above-ground nesters, p=0.192; Figure 10). Small above-ground nesters were not included in this analysis as too few individuals were sampled.

In contrast, post-burn comparison revealed some significant trends in guild combination composition with respect to distance from unburned habitat (medium ground nesters, p=0.042; medium above-ground nesters, p=0.015; large above-ground nesters, p=0.003) (Figure 10). Meanwhile, small (p=0.995) and large (p=0.641) ground-nesting bees did not show a significant influence of distance from the unburned edge post-burn.

4.0 Discussion

Common ecological disturbances, such as wildfires, have the ability to alter habitat community composition in various terrestrial biomes for many taxa including bees (Michener, 2007; Potts *et al.,* 2003b; Potts *et al.,* 2005; Potts *et al.,* 2006; Williams *et al.,* 2010). Fire impact studies on bee communities have until now only looked at small scale burns and generally did not have data at the study site prior to the burn event (Campbell *et al.,* 2007; Moretti *et al.,* 2009; Potts *et al.,* 2001; 2003a; 2003b; 2005; Taylor, 2007; Williams *et al.,* 2010). The general pattern discovered has been one of immediate (i.e. within the first year post-burn) decreases in abundance and species richness but overall increases in Shannon diversity and evenness post-burn (Potts *et al.,* 2003a; 2003b; 2005). Our study of the impacts of a large scale burn showed the same pattern: decreases in abundance and richness with slight, yet significant, increases in Shannon diversity and evenness.

Studies of small-scale burns, as well as ours of a large one, found that bee community composition changes dramatically post burn, as indicated by cluster analyses, PCA, and overall guild proportions. Cluster analyses grouped communities mostly by year illustrating that pre-burn bee communities were more similar to one another as compared to post-burn communities (Figure 4, 5). PCA plots also illustrated differences between community composition by year as well as a strong response by bees to fire (Figure 6, 7) mirroring studies by Moretti *et al.* (2009) and Potts *et al.* (2003b) whose ordination analyses also indicated a strong response of native bee communities to fire.

Earlier work assessed the impact of fire upon different bee guilds and found that a burn had a larger negative impact on bees that nest above ground than those that nest below the ground (Potts *et al.,* 2005; Williams *et al.,* 2010). Our results are consistent with these previous findings. While both below- and above-ground nesting bees decreased in abundance after the fire, the proportional decrease of the latter was slightly, but significantly greater. This was consistent with the results of Williams *et al.* (2010) who found decreases of 15% in above-ground nesters over five years post-burn. It is not surprising that bees whose nest substrate is destroyed in a fire should be more strongly negatively impacted than those that nest underground.

Similarly, Potts *et al.* (2005) found that ground-nesting bees proportionally dominated at all sites of differing post-burn ages, with abundances of ground-nesters being highest in freshly burnt areas, where they represented 57% of all bees one year post-burn. We found greater proportional abundances of ground-nesters (80%). This may be because of differences in fire frequency selecting for ground-nesting bees in areas where episodes of burns are more frequent. Mediterranean fires similar to those described in studies by Potts *et al.*, (2003a; 2003b; 2005) have been smaller and less frequent compared to the fires that tend to occur, both naturally and controlled, in MNP.

Savannah fires have been known to generate intense heat (Bond and van Wilgen, 1996; Neary *et al.*, 1999), though unlike habitats with dense, woody fuel loads, savannah surface fuels are generally sparse and most heat is easily released upwards into the atmosphere (DeBano *et al.*, 1998; Freifelder *et al.*, 1998; Pyne, 1996; Whelan, 1995). As

such, below-ground temperature increases remain small (DeBano, 2000; Neary *et al.*, 1999). High above-ground burn temperatures are common in Argentine savannahs: previous MNP reports (including Heinonen, 2001; Paszko, 2007; 2009) and personal communication with park staff suggested that temperatures had surpassed 1000°C above-ground with relatively rapid fire spread (Freifelder *et al.*, 1998). Consequently, bees utilizing combustible substrates for nesting were not likely to survive intense heat caused by a wildfire, especially not large, intense burns as occurred at our study site. Conversely, fire temperatures decrease rapidly with soil depth (DeBano *et al.*, 1998; DeBano, 2000) and many ground-nesting bees nest at depths of 10-20cm (Christensen, 1994). Thus, even in a large-scale burn where temperatures might be larger than in a smaller burn, significantly lower proportions of above-ground nesters would be expected overall post-burn.

Cane and Neff (2011) experimentally tested the susceptibility of two cavity-nesting bee species to temperature increases and found high survival rates at high temperatures for extended periods of time. Pupal stages of these bees survived best and for longer durations of heat exposure compared to other bee life stages. The wildfires of 2009 in MNP occurred following the dry (winter) period when the majority of bees are at immature stages of development. Thus, most ground-nesting bees at MNP are expected to survive a wildfire and take advantage of newly opened ground nesting habitat immediately post-burn.

Due to the large size of the unplanned burn at our study site, we were able to assess the impact of distance from the edge of the fire on bee community responses. Pre-burn data were used as controls for post-burn data and showed no significant differences in variation among bee communities with increasing distance from future fire edges. However, after the fire, ground-nesting bee abundance was positively correlated with distance from the unburned edge. This was likely due to a combination of higher below-ground nester survival and a decrease in available nesting resources at the heart of the fire for above-ground nesting bees.

Nesting resources become limited for above-ground nesters within the heart of a recent burn compared to unburned habitat just outside the fire margin where nesting materials, such as wood and stems, are more readily available. This may explain why above-ground nesters of all body sizes were found in greater proportional abundances closer to fire edges immediately post-burn. Our findings suggest that above-ground nesters are unable to colonize recently burned habitat as quickly as ground-nesters regardless of survival rates *in situ*. Steffan-Dewenter and Tscharntke (2001) reported that above-ground nesters continue increasing in abundance and species richness up to five years post-burn since freshly burned habitats lack nesting sites for these bees immediately after a fire. Other studies have shown that required nesting resources for these bees are limited post-burn, slowing recolonization of above-ground nesters during early successional stages (Potts *et al.*, 2003a; 2005; Williams *et al.*, 2010).

We expected that bees with larger body sizes would be less impacted by distance from the fire edge than were smaller bees because of their increased mobility (Araujo *et al.,* 2004; Cane, 1987; Greenleaf *et al.,* 2007). This pattern should occur independently of nesting guild because even if above-ground nesters lost their nest sites in the fire, larger members of that guild should be able to forage deeper into the previously burned area than a smaller one. However, we found the opposite, larger bees were proportionately more abundant closer to the edge. Looking more closely, we assessed the impact of distance from the unburned edge upon combinations of nest site and bee size guilds we found that all above-ground nesters, both medium and large (sample sizes were too small for analysis of small above-ground nesters), showed a significant decrease in proportional abundance with increasing distance from the burn edge. Most above-ground nesters would not be able to survive a large-scale burn and would therefore be emerging from unburned habitat. The data suggest that they did not fly as deeply into the burned area as expected and were found proportionately more commonly nearer the edge of the burn. The decline in above-ground nesters as distance increased also suggests that large-scale fires will have an even greater impact upon above-ground nesters than do smaller-scale burns.

The only significant response for ground-nesting bees was that medium-sized bees increased in abundance with distance from the unburned edge while small and large ground nesters showed no significant difference. In contrast to bees that nest above the ground, ground-nesters are generally the most abundant and diverse guild within most

habitats, especially in grassland and savannah habitats where open ground is readily available (Michener, 2007). Combined with their higher likelihood of wildfire survival (Cane and Neff, 2011), such bees may be able to exploit newly cleared ground post-burn more rapidly than can above-ground nesting bees. We expected that larger ground-nesting bees would be those most able to travel farthest into recently burned habitat while smaller ground nesters would be limited in foraging range. Medium-sized ground-nesters followed the expected positive correlation with respect to distance. However, small and large ground-nesting bees remained unaltered by foraging distance post-burn. Collectively, this indicates that ground-nesting bees, regardless of size, are least affected by distance from foraging or nesting resources. These finding are consistent with the study by Williams *et al.* (2010) which described a 47% decrease in above-ground nesting bee abundance as isolation from natural habitat increased and that body size was not important for determining bee responses to (fire) disturbances.

Since this is the first study of the impacts of a large-scale burn upon bees, many areas for further work can be suggested. Greater replication, a greater range in distances from fire edges, and a longer term study with multiple years of pre- and post-burn data should strengthen our findings as well as provide insight into native bee community succession within savannah habitat. Finally, exploring temporal differences between burns upon native bee communities, such as comparisons between winter and spring/summer burns would provide greater understanding to how these bee communities

respond to large-scale burns in savannah habitat and inform community restoration efforts.

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Tables and Figures

Table 1. Trap site collection data for 5 traps set within Mburucuyá National Park during a 2 year period; collection of specimens between April 5 to October 17, 2009 and from April 9 to October 28, 2010.

Trap	Site Location	GPS Coordinates		Time Since Previous Burn (years)	Distance from Nearest Unburned Edge (km)
1	Santa Teresa	S 28°01.617	WO58°02.750	2	0.38
2	2 chico	S 28°01.450	WO58°02.733	6	0.45
3	Santa Teresa	S 28°01.233	WO58°02.367	2	0.90
4	Santa Teresa	S 28°01.183	WO58°02.150	2	1.20
5	Tung	S 28°01.150	WO58°02.083	6	1.65

Table 2. Total number bee specimens and species collected over a two-year period from 5 traps set in Mburucuyá National Park. Body size of species based on specimen measurements (small = small sized bees, medium = medium sized bees, large = large sized bees). Guild characterization of species based on known nesting behaviour (cavity = cavity-nesting, clepto = cleptoparasite, ground = ground-nesting, stem = stem-nesting, wood = wood-nesting).

				2009					2010					
Genus, species	PCA Acronyms	Nesting Guild Association	Body Size	Trap 1	Trap 2	Trap 3	Trap 4	Trap 5	Trap 1	Trap 2	Trap 3	Trap 4	Trap 5	Total Individuals
Anthrenoides meloi (Urban)	A.meloi	ground	medium					1						1
Anthrenoides sp.1	Anoides1	ground	medium					1						1
Anthrenoides sp.2	Anoides2	ground	medium				1							1
Apis mellifera (Linnaeus)	A.melli	cavity	large	1		7	2	9		2	3	7	9	40
Augochlora amphitrite (Schrottky)	A.amphi	wood	medium	1	1	3	13	6			1	2	2	29
Augochlora phoemonoe (Schrottky)	A.phoem	wood	medium			7	7	7	1	1	1	1	1	26
Augochlorella acarinata (Coelho)	A.acari	ground	medium			1	1						1	3
Augochlorella ephyra (Schrottky)	A.ephyr	ground	medium	1		1	9	9					4	24
Augochloropsis sp.8	Augo8	ground	medium										2	2
Augochloropsis sp.B	AugoB	ground	medium			1	4	6			4		16	31
Augochloropsis sp.C	AugoC	ground	medium		1		2	2					4	9
Augochloropsis sp.D	AugoD	ground	medium			1								1
Augochloropsis sp.F	AugoF	ground	medium				1						6	7
Augochloropsis sp.G	AuoG	ground	medium	1				1					14	16
Augochloropsis sp.H	AugoH	ground	medium				2	1				1	4	8
Augochloropsis sp.I	AugoI	ground	medium	1		1	4						1	7
Augochloropsis sp.J	AugoJ	ground	medium	1		1		2		1	1		4	10
Augochloropsis sp.K	AugoK	ground	medium	2		2	2	4				1	16	27
Augochloropsis sp.L	AugoL	ground	medium	1										1
Augochloropsis sp.N	AugoN	ground	medium									1		1
Augochloropsis tupacamaru (Holmberg)	A.tupac	ground	medium			1	1	1					1	4
Ceratina sp.1	Ctina1	stem	medium	2			2						2	6
Ceratina sp.2	Ctina2	stem	medium	1		1		1					3	6
Ceratina sp.3	Ctina3	stem	medium	2		10	8	5					2	27
Ceratina sp.4	Ctina4	stem	small				1	1						2
Ceratina sp.5	Ctina5	stem	---	2	1	1								4
Ceratina sp.7	Ctina7	stem	small			1								1
Coelioxys praetextata (Haliday)	C.praet	clepto	large										2	2
Coelioxys sp.1	Coexys1	clepto	large	1			1							2
Epanthidium autumnale (Schrottky)	E.autum	ground	medium										1	1

				2009					2010					
Genus, species	PCA Acronyms	Nesting Guild Association	Body Size	Trap 1	Trap 2	Trap 3	Trap 4	Trap 5	Trap 1	Trap 2	Trap 3	Trap 4	Trap 5	Total Individuals
Epanthidium erythrocephalm (Schrottky)	E.eryth	ground	large										1	1
Exomalopsis sp.1	Exo1	ground	medium				1				1			2
Hypanthidioides argentina (Urban)	H.argen	ground	medium					1						1
Hypanthidium sp.1	Hypan1	ground	medium					1					2	3
Lasioglossum (Dialictus) brunerlellum (Cockerell)	L.brun	ground	medium		1	1	2							4
Lasioglossum (Dialictus) sp.1	Dia1	ground	small	11	4	57	70	33			1		4	180
Lasioglossum (Dialictus) sp.2	Dia2	ground	small	7		5	13	9						34
Lasioglossum (Dialictus) sp.6	Dia6	ground	small				1							1
Lasioglossum (Dialictus) spinolae (Reed)	L.spino	ground	small			1								1
Megachile (Acentron) sp.1	MegAce1	stem	large						1		1			2
Megachile (Chrysosarus) sp.1	MegChry1	stem	large				1							1
Megachile (Chrysosarus) sp.2	MegChry2	stem	large	2			3	1					1	7
Megachile (Cressoniella) sp.1	MegCres1	stem	large					1						1
Megachile (Cressoniella) sp.2	MegCres2	stem	large				1							1
Megachile (Leptorachis) sp.1	MegLept1	stem	large	1			2					1		4
Megachile (Leptorachis) sp.2	MegLept2	stem	large			2	3	2						7
Megachile (Melanosarus) sp.1	MegMel1	stem	large					1						1
Megachile (Moureapis) sp.1	MegMour1	stem	large				1	2						3
Megachile (Pseudocentron) sp.1	MegPse1	stem	large				1	1					2	4
Psaenythia magnifica (Holmberg)	P.magni	ground	large				1	4			1	3	19	28
Psaenythia sp.2	Psaeny2	ground	medium				2	1						3
Psaenythia sp.3	Psaeny3	ground	medium			1	1							2
Pseudagapostemon pampeanus (Holmberg)	P.pampe	ground	medium	6	4	6	25	4			1	2	2	50
Pseudagapostemon sp.2	Pagapos2	ground	medium		2									2
Pseudaugochlora sp.2	Pseud2	ground	large	1				1	1		1			4
Rhinocorynura sp.1	Rhino1	ground	medium	1	1	1	3	3				6	5	20
Rhophitulus sp.1	Rhoph1	ground	small			2	3	1						6
Rhophitulus sp.2	Rhoph2	ground	small			1	1					1		3
Sphecodes sp.1	Speco1	clepto	small				2							2
Sphecodes sp.2	Speco2	clepto	medium				2	1						3
Svastrides sp.1	Svast1	ground	large									1		1
Temnosoma sp.1	Temno1	clepto	medium								1	1	3	5
Thectochlora basiatra (Strand)	T.basia	ground	medium	6	2	11	11	15		1		5	32	83
Xylocopa splendidula (Lepeletier)	X.splen	wood	large			1								1
Grand Total				52	17	128	211	139	3	5	17	33	166	771

Table 3. Comparison of diversity indices for samples collected over a two year period from 5 traps set within Mburucuyá National Park. Significance values obtained using chi square tests ($X^2_{4,1}$) for number of specimens ($p<0.001$) and species richness ($p=0.023$). Using variance of H', a two-tailed t-test ($\alpha = 0.05$) was used to determine significant differences between years for Shannon diversity ($p<0.001$) and species evenness ($p<0.001$).

Year	Number of Specimens (N)	Species Richness (S)	Shannon Diversity (H')	varH'	df	Evenness (J')	D	P
2009	547	56	2.8435	0.0001	340	0.7064	0.3044	0.1237
2010	224	37	2.9967	0.0004	-	0.8299	0.2525	0.1466
Total (combined years)	771	64	-	-	-	-	0.2105	0.0771

Table 4. Bees collected and sorted by guild based on nesting resource requirements for each trap within Mburucuyá National Park over a two-year period for below-ground and above-ground nesting bees. Statistical comparison of individual guilds using chi square tests (Minitab Inc., 2010) gave $p<0.001(X^2_{3,1})$ in all cases. Note: ground= ground-nesting, stem= stem-nesting, wood= wood-nesting, cavity= cavity-nesting.

Year	Guild		Traps					Total	
			Trap 1	**Trap 2**	**Trap 3**	**Trap 4**	**Trap 5**	**Abundance**	**%**
2009	ground	below ground	39	15	95	161	101	411	**76**
	stem	above ground	10	1	15	23	15	64	**24**
	wood		1	1	11	20	13	46	
	cavity		1	0	7	2	9	19	
Total			51	17	128	206	138	**540**	100
			Trap 1	**Trap 2**	**Trap 3**	**Trap 4**	**Trap 5**	**Abundance**	**%**
2009	ground	below ground	1	2	10	21	139	173	**80**
	stem	above ground	1	0	1	1	10	13	**20**
	wood		1	1	2	3	3	10	
	cavity		0	2	3	7	9	21	
Total			3	5	16	32	161	**217**	100

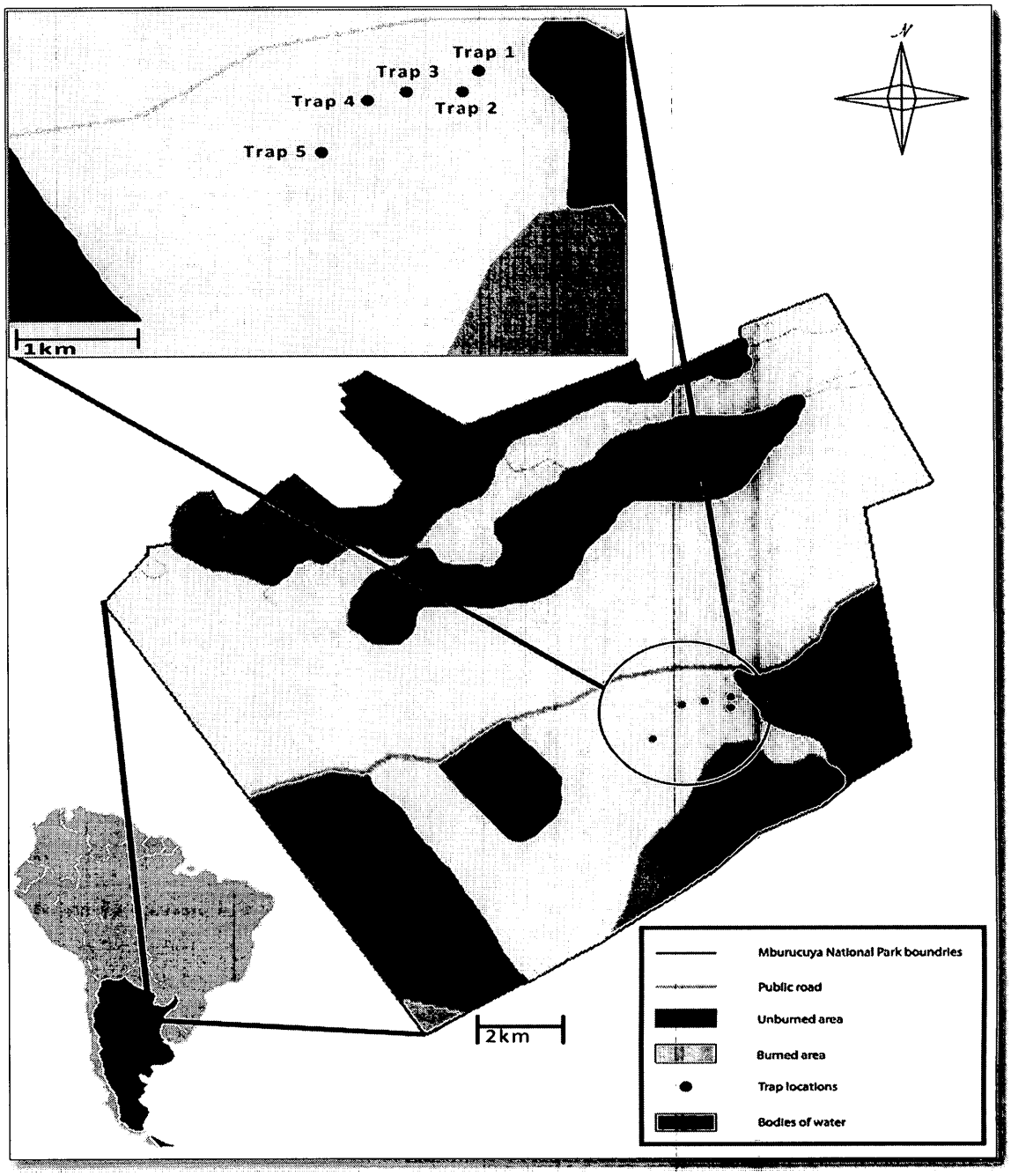


Figure 1. Map of Mburucuyá National Park illustrating unburned areas within park (green) after large-scale burn occurred in late October, 2010. 5 trap locations (red) within burned savannah habitat with same location placement from April to October in 2009 and 2010. Map generated using Google Earth (version 5.1.3533.1731).

Figure 2. Photo of a Townes style malaise trap (Sante Traps) used for sampling in Mburucuyá National Park within Yatay palm savannah habitat during dry winter season in 2010.

Figure 3. Photo illustrating park staff setting malaise traps within savannah habitat containing a greater density of Yatay palm trees and shrubs in Mburucuyá National Park during summer season in 2010.

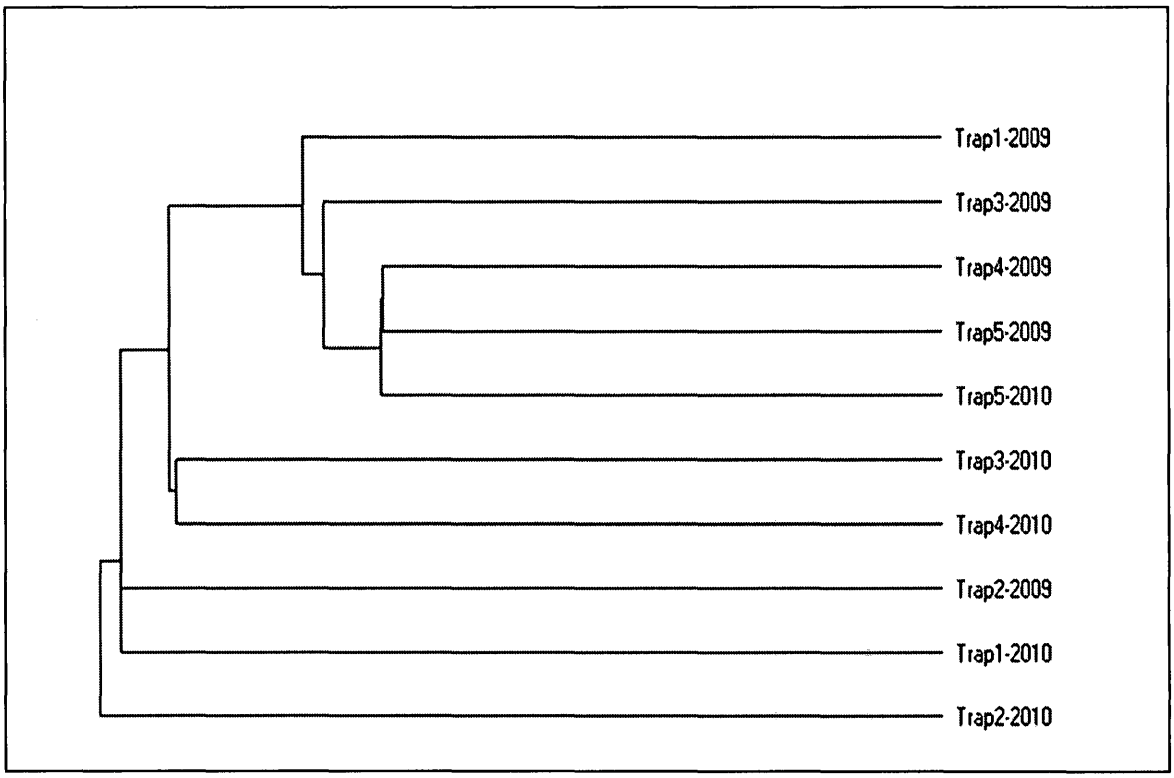


Figure 4. Single linkage Jaccard cluster analysis illustrating similarity of species composition (using Community Analysis Package 3.2; Henderson and Seaby, 2004) to describe trap similarities among 5 traps within Mburucuyá National Park for 2009 and 2010.

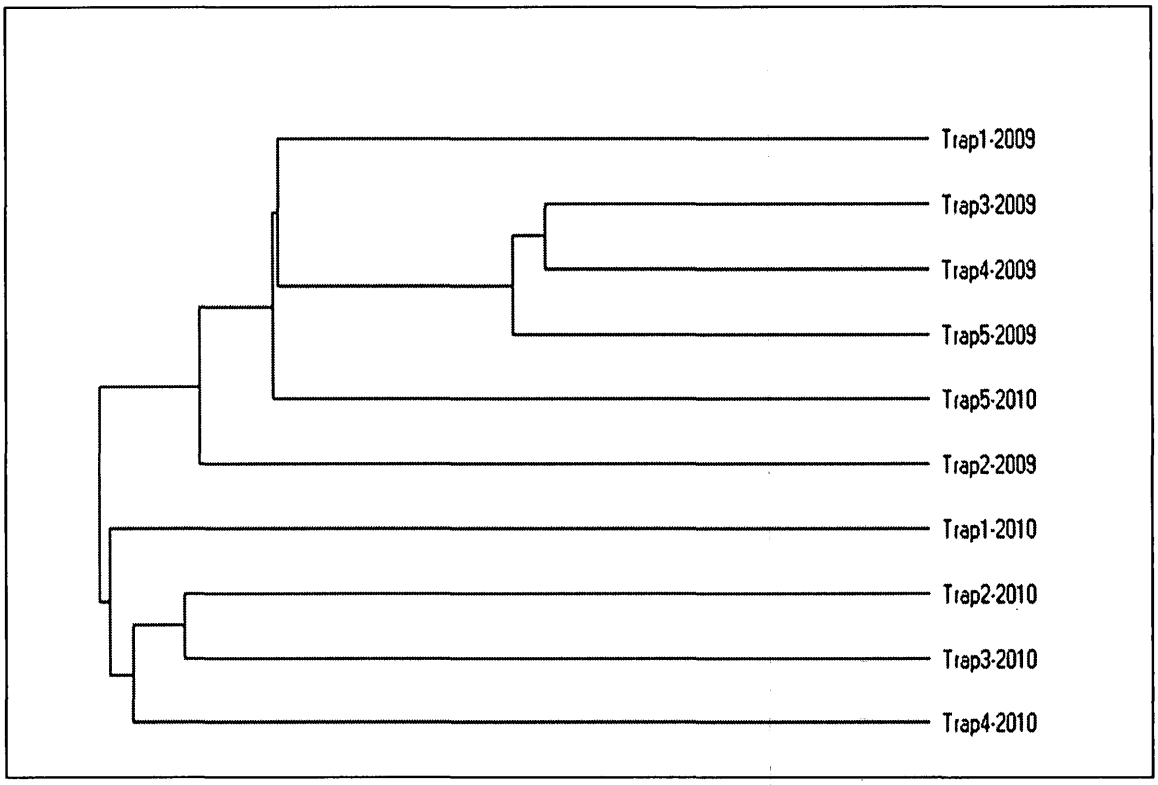


Figure 5. Single linkage Bray-Curtis cluster analyses illustrating dissimilarity between abundance of species within each trap between years (using Community Analysis Package 3.2; Henderson and Seaby, 2004) for data collected from 5 traps within Mburucuyá National Park for 2009 and 2010.

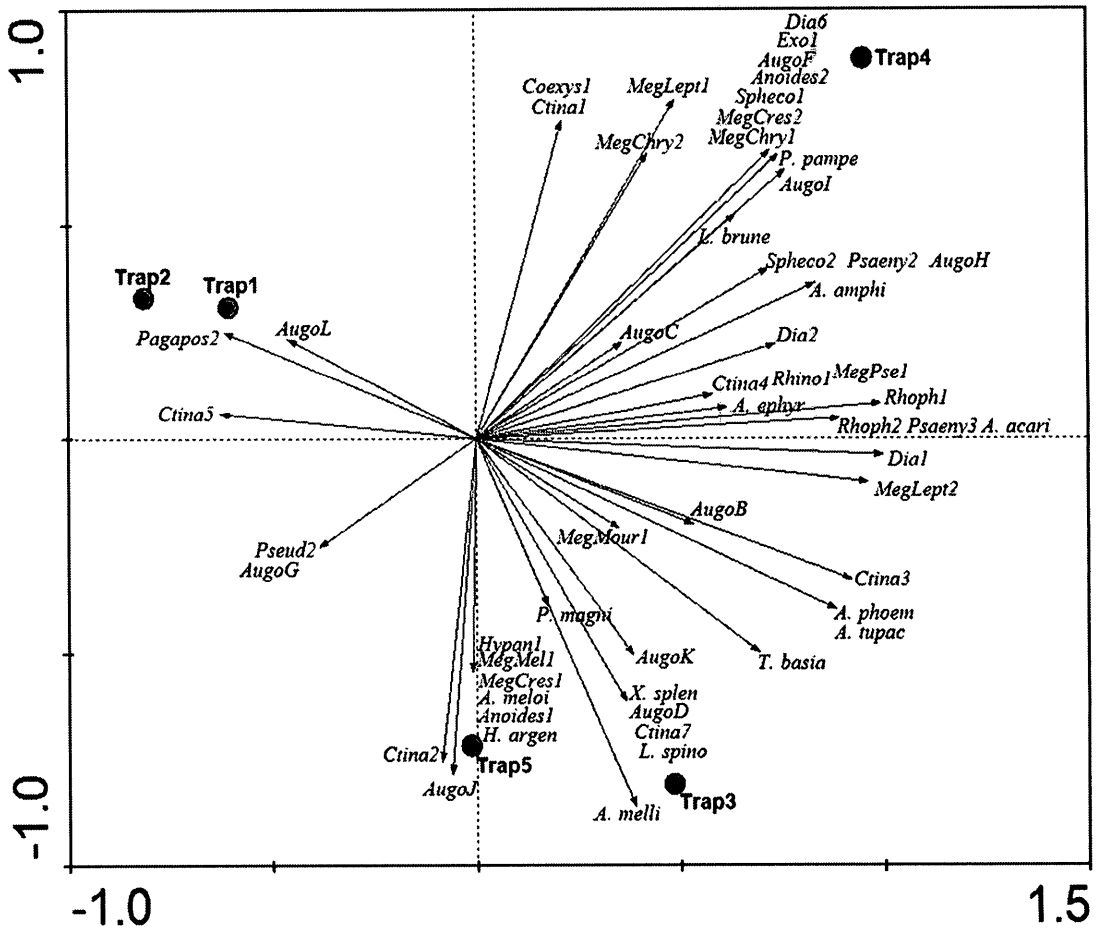


Figure 6. Principle Component Analysis (PCA) plot showing relationship between community variability between trap sites set within Mburucuyá National Park for 2009 pre-burn data. Species variation within the community is represented along the x-axis while species variation in response to fire is represented along the y-axis. Circles represent malaise trap locations and solid lines represent bee species. Cumulative percentage variance of species data explained is 88% for axis 1 and 94.6% for axis 2. PCA generated using Canoco 4.5 (Lepš and Šmilauer, 2003).

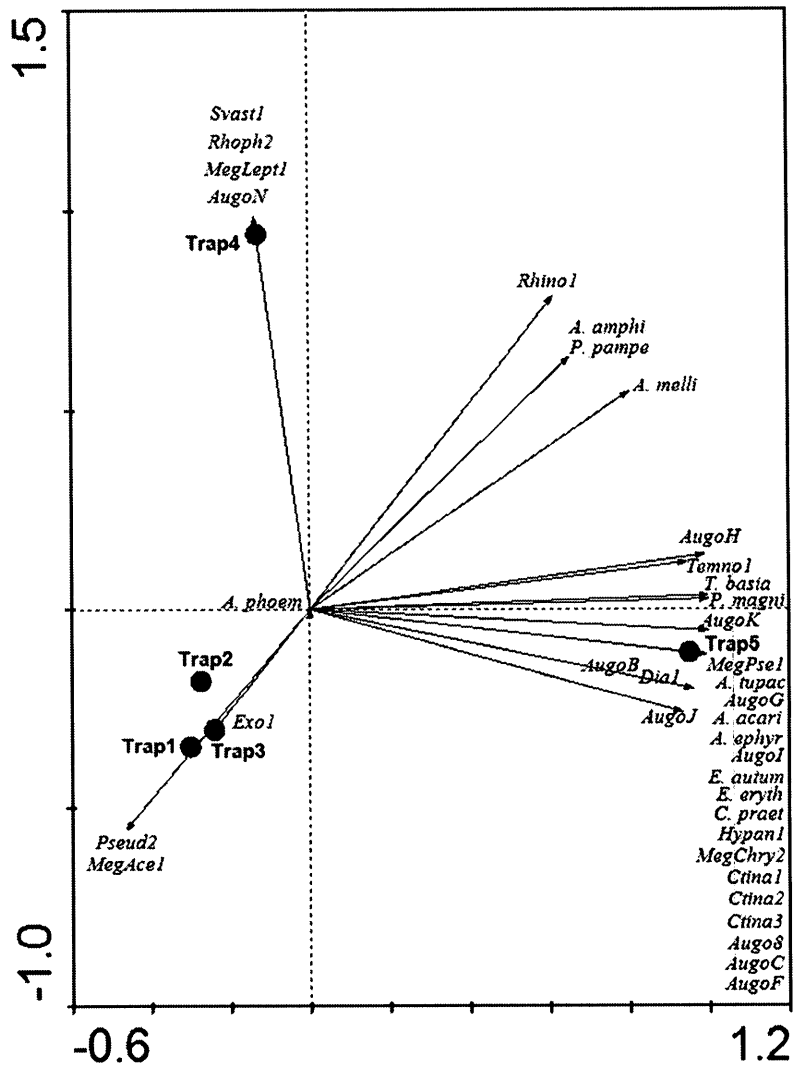


Figure 7. Principle Component Analysis (PCA) plot showing relationship between community variability between trap sites set within Mburucuyá National Park for 2010 post-burn data. Species variation within the community is represented along the x-axis while species variation in response to fire is represented along the y-axis. Circles represent malaise trap locations and solid lines represent bee species. Cumulative percentage variance of species data explained is 96.5% for axis 1 and 99% for axis 2. PCA generated using Canoco 4.5 (Lepš and Šmilauer, 2003).

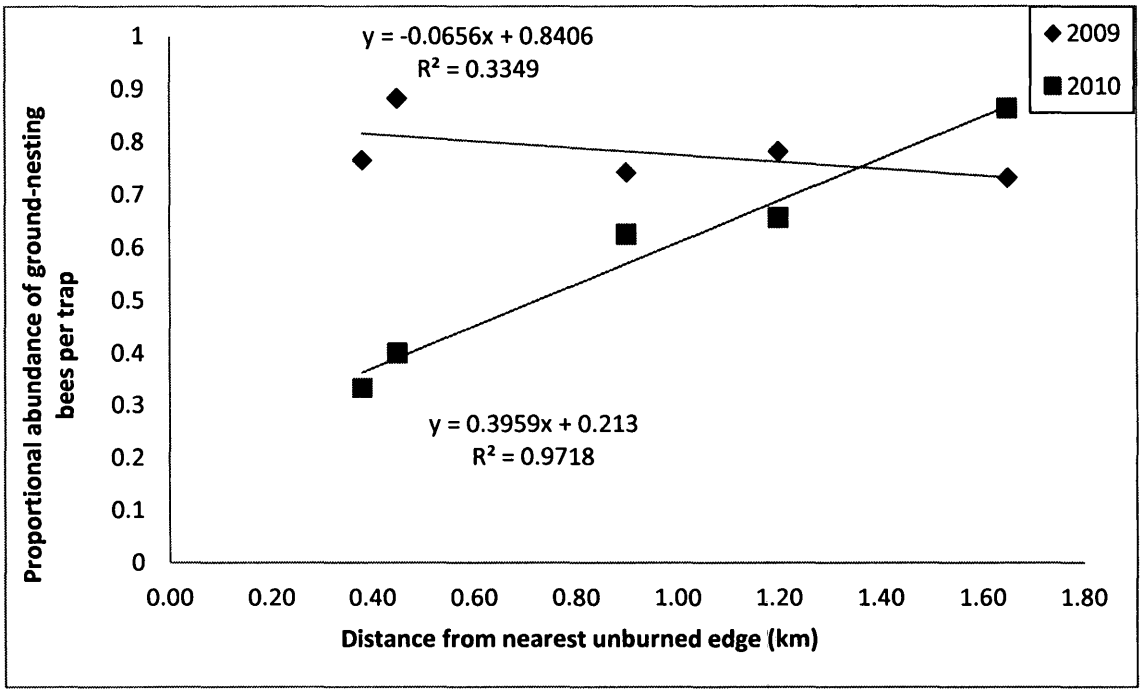


Figure 8. Scatter plot of ground-nesting bee proportional abundances with linear trendlines for unburned (2009) and burned (2010) years at increasing distances from nearest unburned edge within Mburucuyá National Park. Comparison of slope significance between years for ground-nesting bees determined using SPSS 20 (IBM SPSS Inc., Chicago, IL, USA) where $p<0.001$ (df=6, two-tailed t-test). Comparison to zero slope resulted in $p=0.307$ for 2009 (df=3, two-tailed t-test).

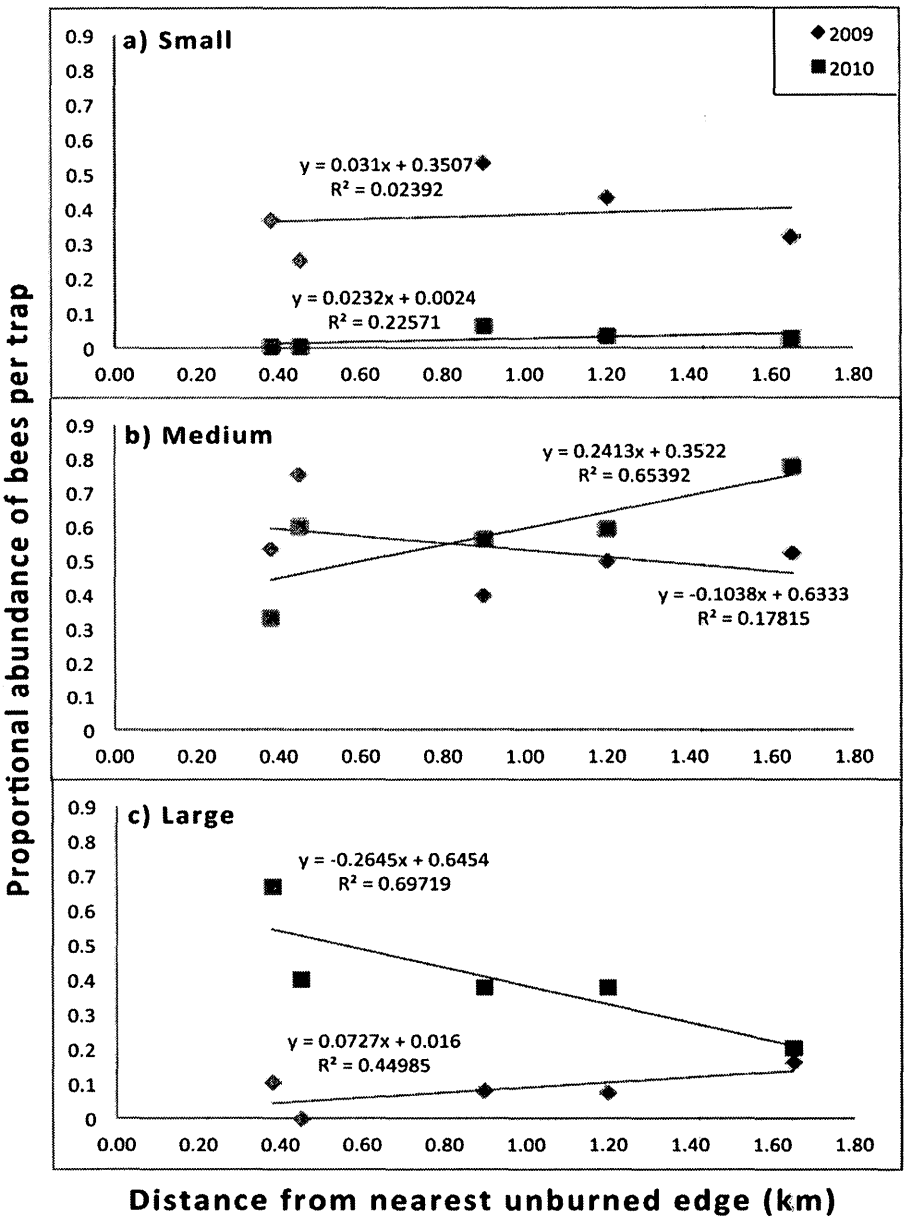


Figure 9. Scatter plot of proportional bee abundances based on body size with linear trendlines for unburned (2009) and burned (2010) years at increasing distances from nearest unburned edge within Mburucuyá National Park and comparison of slopes (df=6, two-tailed t-test) for a) small bees, p=0.949; b) medium bees, p=0.080; and c) large bees, p=0.023; using SPSS 20 (IBM SPSS Inc., Chicago, IL, USA). Comparison to zero slope for 2009: a) small bees p=0.804; b) medium bees p=0.479; and c) large bees p=0.215 (df=3, two-tailed t-test).

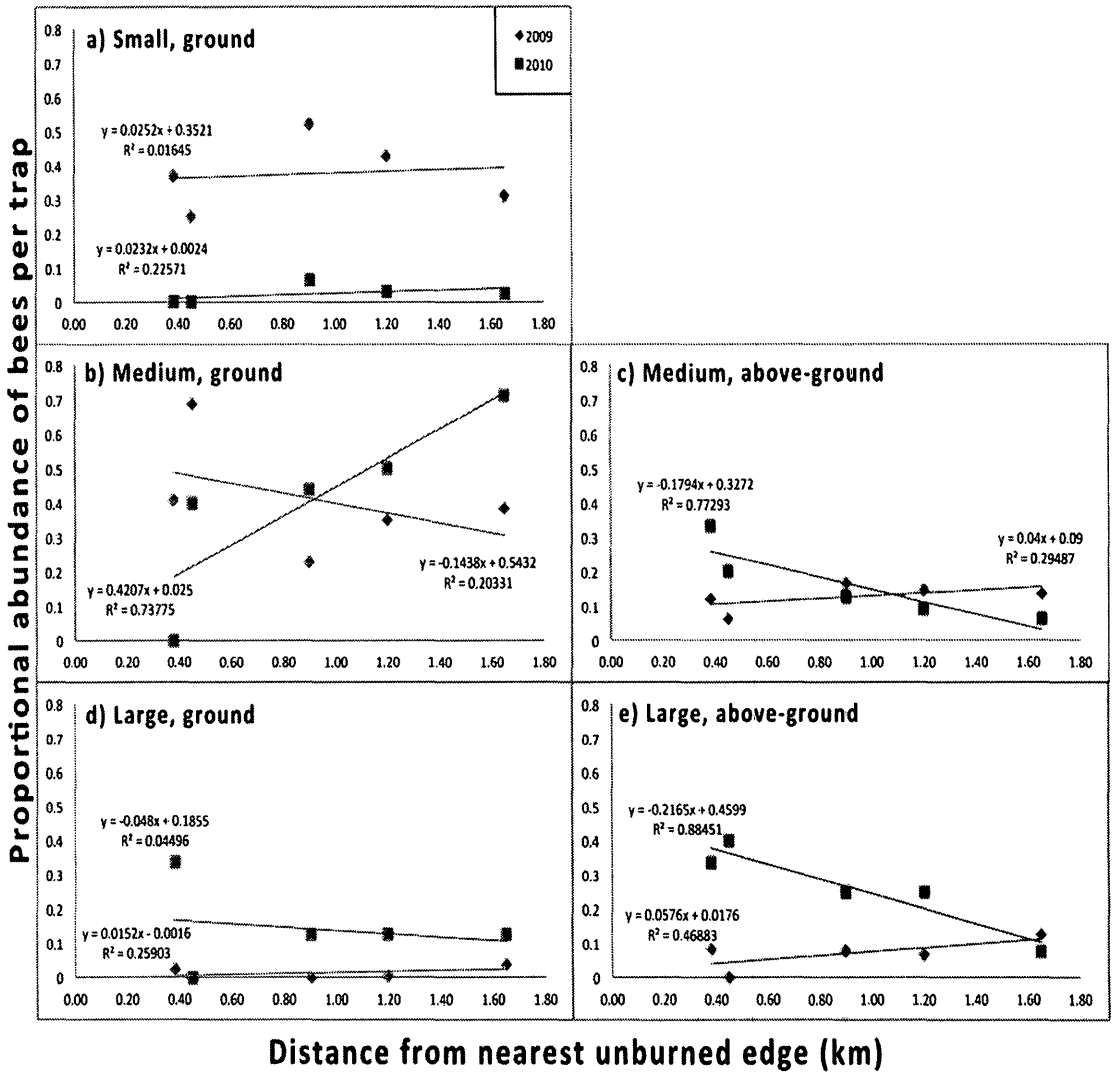


Figure 10. Proportional abundance scatter plots of below-ground and above-ground bees based on body size with linear trendlines for unburned (2009) and burned (2010) years at increasing distances from the nearest unburned edge within Mburucuyá National Park. Comparison to zero slope for 2009 data (df=3, two-tailed t-test) and comparison of slopes between pre- and post-burn samples (df=6, two-tailed t-test) were determined using SPSS 20 (IBM SPSS Inc., Chicago, IL, USA), respectively: a) small ground-nesting bees p=0.845, p=0.995; b) medium ground-nesting bees p=0.443, p=0.042; c) medium above-ground nesting bees, p=0.329, p=0.015; d) large ground-nesting bees, p=0.381, p=0.641; and e) large above-ground nesting bees, p=0.192, p=0.003.

Appendix A: Burn History for Mburucuyá National Park

Table 5. Summary of burn history since establishment of Mburucuyá National Park in 1996 to 2010. Note: WF = wildfire, PB = prescribed burn.

	Year														
Site Locations	Prior to 1997	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
15	WF (1994)		WF					WF				PB		WF	
3	WF (1994)		WF			WF?		WF				PB		WF	
Naranjo														WF	
1	WF (1992, 1995)		WF	WF		WF (1ha)	PB		PB						
Rincon	WF (1996)					WF (6ha)	PB		PB			PB			
Quebrachal														WF	
18, Maizal-cue	WF (1996)	WF	WF					PB						WF	
20														WF	
10														WF	
9 (grande, chico)	WF (1996)	WF		WF					PB					WF	
8														WF	
5	WF (1996)	WF	WF		WF (0.5ha)	PB		PB			WF?	PB	WF	WF	
7														WF	
14	WF (1996)		WF	WF		WF		WF, PB				PB			
13	WF (1996)		WF	WF		WF		WF, PB		WF		PB			
Santa Maria (11, 12)	WF (1993, 1996)	WF	WF			WF			PB			PB?		WF	
16	WF (1996)							PB?		WF				WF	
17	WF (1995, 1996)	WF?	WF?	WF, PB		WF, PB		PB	PB			PB			PB
2 grande (West side)	WF (1996)	PB	WF	WF		PB		PB	PB			PB		WF	
2 chico (East side)	WF (1996)	PB	PB	PB		PB	PB	PB						WF	
Tung		PB		WF		WF		WF						WF	
Santa Teresa			WF,PB	WF, PB		WF, PB			PB			PB		WF	
4, Piquete Cruz, 1 chico, 1 grande			WF	WF	WF (3ha)	WF			PB			PB		WF?	
6									PB		WF?			WF	

Appendix B: Cluster Analyses Matrixes

Table 6. Jaccard dendrogram data matrix illustrating similarity of species present in Mburucuyá National Park using Community Analysis Package 3.2 (Henderson and Seaby, 2004) for trap similarity between 5 traps in 2009 and 2010.

Jaccard Dendrogram Matrix of Working Data										
	Trap1 2009	Trap2 2009	Trap3 2009	Trap4 2009	Trap5 2009	Trap1 2010	Trap2 2010	Trap3 2010	Trap4 2010	Trap5 2010
Trap1-2009										
Trap2-2009	0.250									
Trap3-2009	0.412	0.241								
Trap4-2009	0.333	0.171	0.435							
Trap5-2009	0.375	0.162	0.386	0.490						
Trap1-2010	0.043	0.000	0.034	0.024	0.057					
Trap2-2010	0.136	0.083	0.148	0.075	0.118	0.167				
Trap3-2010	0.222	0.167	0.219	0.186	0.243	0.250	0.231			
Trap4-2010	0.250	0.211	0.242	0.262	0.231	0.063	0.200	0.300		
Trap5-2010	0.417	0.182	0.390	0.438	0.488	0.031	0.133	0.273	0.294	

Table 7. Bray-Curtis dendrogram data matrix illustrating dissimilarity between abundance of species in Mburucuyá National Park using Community Analysis Package 3.2 (Henderson and Seaby, 2004) for data collected from 5 traps in 2009 and 2010.

Bray-Curtis Dendrogram Matrix of Working Data										
	Trap1 2009	Trap2 2009	Trap3 2009	Trap4 2009	Trap5 2009	Trap1 2010	Trap2 2010	Trap3 2010	Trap4 2010	Trap5 2010
Trap1-2009										
Trap2-2009	0.623									
Trap3-2009	0.556	0.807								
Trap4-2009	0.658	0.877	0.327							
Trap5-2009	0.571	0.833	0.356	0.377						
Trap1-2010	0.964	1.000	0.985	0.991	0.972					
Trap2-2010	0.895	0.909	0.925	0.963	0.931	0.750				
Trap3-2010	0.826	0.824	0.876	0.895	0.821	0.700	0.636			
Trap4-2010	0.718	0.760	0.752	0.836	0.709	0.944	0.789	0.680		
Trap5-2010	0.752	0.880	0.735	0.735	0.561	0.988	0.942	0.847	0.719	

Appendix C: Mburucuyá National Park Sectors

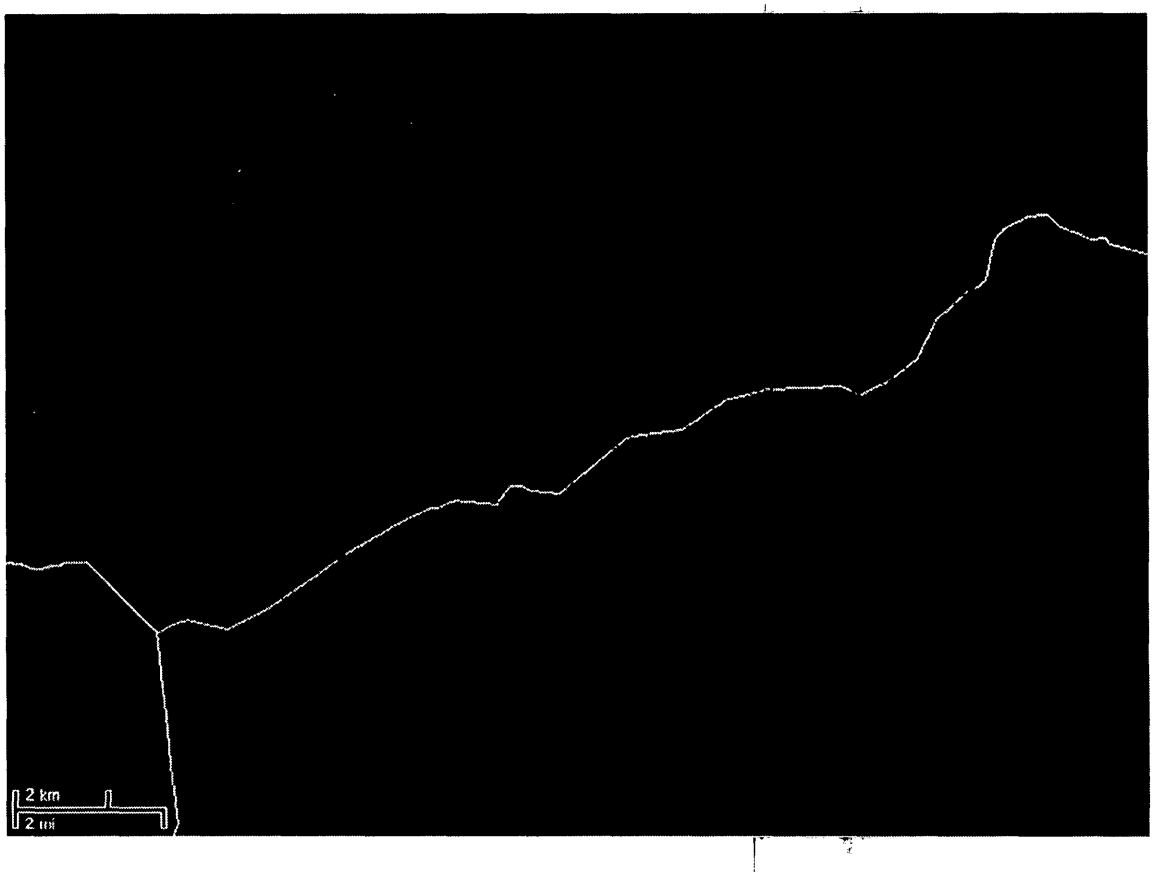
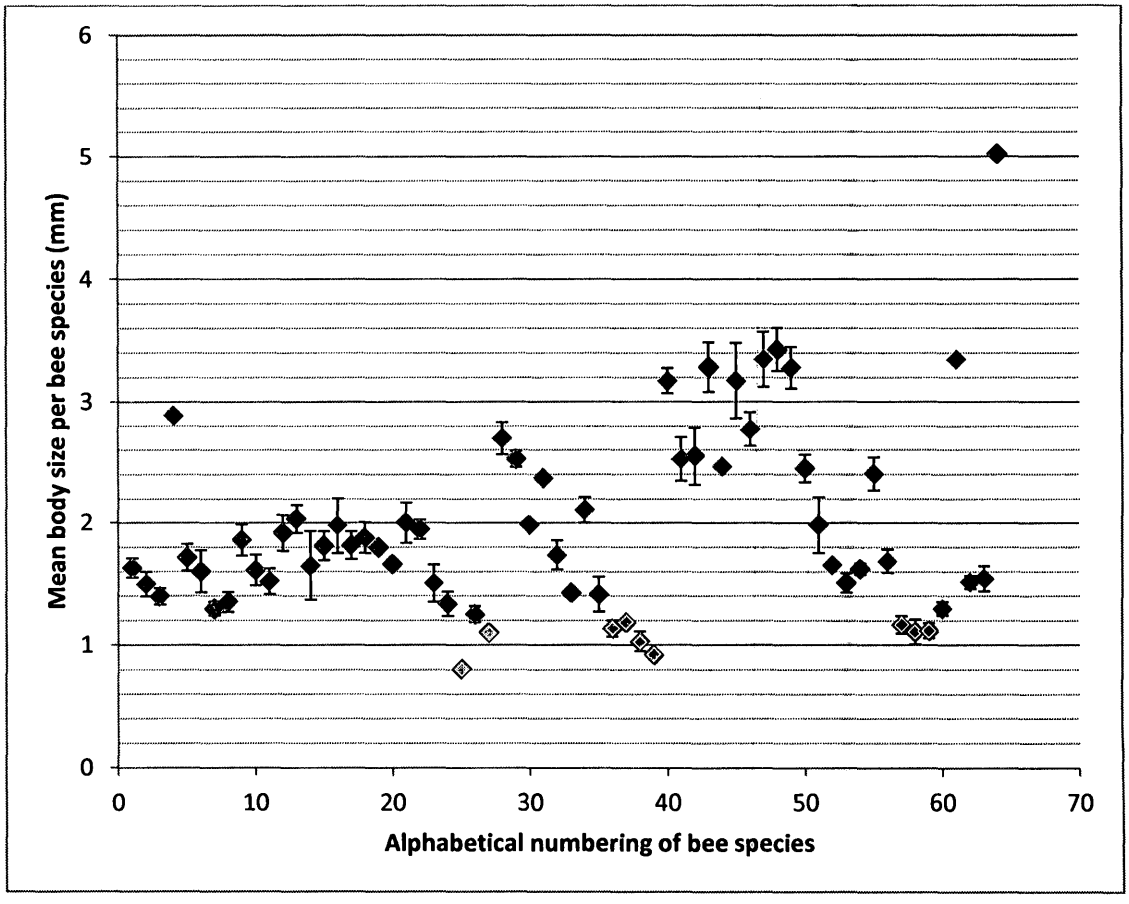


Figure 11. Mburucuyá National Park section numbers and common names correlating to burn history for prescribed burns and wildfires. Park bisected by public road. Map generated using Google Earth (version 5.1.3533.1731).

Appendix D: Bee Body Size Grouping

Figure 12. Scatterplot spectrum of mean body size for bees collected in Mburucuyá National Park. Bees sorted into 3 size categories based on error bar overlap: small bees (<1.24mm), medium bees (1.24mm-2.23mm), large bees (>2.23mm), and solid black (ambiguous size category).



Appendix E: Breakdown of Statistical Analysis

Diversity Indices

Consistency between indices used among various biodiversity and conservation studies increases comparability to similar studies, thus bee community composition for MNP was analyzed by comparing total number of individuals, species richness, diversity, and evenness measures of samples collected each year. Total number of individuals (N) refers to the total number of individuals sampled per trap each year. Species richness (S) is the total number of species collected for each sample each year. Chi square tests were used to test for significant difference between years for total number of specimens (N) and Species Richness (S) using Minitab 16 (Minitab Inc., 2010). This method was also used to determine significant differences between guild compositions for each year of study.

Diversity (H') and Evenness (J') are indices based on proportional abundances of species and take into account species richness and evenness without making assumptions based on species abundance distributions (Magurran, 1988). The Shannon index does assume that all species are represented in a sample and that those individuals have been randomly sampled from a larger population (Magurran, 1988), therefore permitting combining of trap samples within MNP.

Diversity is measured by the Shannon Index of Diversity (Magurran, 1988; Magurran, 2004; Zar, 1999):

Shannon Index of Diversity: $H' = -\sum p_i \ln p_i$ (1)

Where p_i is the proportion of individuals found in the i^{th} species (Magurran, 2004). Shannon index values tend to range from 0 to 4 with higher values indicative of greater number of species present (Magurran, 2004). The variance of H' is utilized to calculate significant differences between samples and can be calculated using (corrected from Magurran, 1988):

Variance of Shannon index: $$\text{var } H' = \frac{[\sum pi\, ln(pi)^2 - \sum pi\, ln(pi)\ ]^2 / N}{N^2} + \frac{S-1}{2N^2}$$ (2)

Where N is the total number of individuals in the sample and S is the total number of species (Magurran, 1988). Significant differences between diversity variances are calculated using the t-test statistic and is calculated using (Magurran, 1988):

t-test statistic: $$t = H'_1 - H'_2 / (varH'_1 + varH'_2)^{1/2}$$ (3)

Where H'_1 is the diversity of sample 1 and $varH'_1$ is its associated variance. The degrees of freedom (df) are calculated using (Magurran, 1988):

Degrees of Freedom: $$df = (varH'_1 + varH'_2)^2 / (varH'_1)^2 / N_1 + (varH'_2)^2 / N_2$$ (4)

Where N_1 and N_2 correspond to the total number of individuals used to calculate $varH'_1$ and $varH'_2$, respectively.

Evenness (J') is a constant of the Shannon diversity and is measured as (Magurran, 1988):

Evenness: $$J' = H' / \ln S$$ (5)

Where S is equal to the total number of species in a sample. Values for J' range from 0 to 1 whereby values approaching 1 increasing become more even in abundance (Magurran, 2004).

Similarity Indices

Clustering analyses may allow for visual comparison of similarity or dissimilarity of samples. The Community Analysis Package 3.2 (Henderson and Seaby, 2004) allows for agglomerative data classification into groups based on similarity.

The Jaccard index is a binary coefficient used to compare the similarity and diversity by looking at species present between sample sets (Krebs, 1999). The Jaccard index was selected for this study as it weights all species collected equally (Krebs, 1999; Magurran, 2004).

Jaccard Index: $$Sj = \frac{a}{a+b+c} \quad (6)$$

Where Sj is equal to Jaccard's similarity coefficient and a, b, and c refer to a defined presence/absence matrix (Krebs, 1999).

To analyze abundance measure, the Bray-Curtis measure for distance coefficients providing values from 0 to 1 where values closer to 0 are most alike (Krebs, 1999).

Bray-Curtis Measure: $$B = \frac{\sum_{i=1}^{n} |Xij - Xik|}{\sum_{i=1}^{n} (Xij + Xik)} \quad (7)$$

Where B is equal to the Bray-Curtis measure of dissimilarity, Xij and Xik are equal to the

number of individuals in species *i* in each sample *(j, k)*, and *n* is equal to the number of species in the samples (Krebs, 1999).

Ordination

Analyzing community composition can be challenging when various underlying factors, such as environmental conditions, are able to influence how communities react to those changes (Lepš and Šmilauer, 2003). Those changes may not be easily detected; therefore, assessing overall species composition of a community in order to visualize and understand environmental conditions becomes important. Ordination is a method used to arrange species and samples along a reduced number of axes in a way that similar or dissimilar species or samples are placed closer together or farther apart, respectively (Krebs, 1999; Lepš and Šmilauer, 2003). Though several methods of ordination are available, each method becomes a useful tool for illustrating patterns in community data.

Principle component analysis (PCA) is an ordination method that plots axes through the greatest corresponding variability within a data set that can be explained by the samples (Lepš and Šmilauer, 2003). Following Potts *et al.* (2006) and Taylor (2007), Canoco 4.5 (Lepš and Šmilauer, 2003) was used to generate a PCA diagram in order to visualize patterns between all species and trap sites. Data was plotted without differential weighting of any species or samples in order to determine how community composition differed between burned and unburned years.

Significance of Proportional Abundance by Guild Composition

Significant differences between slopes for each sampled year by trap were determined using Zar (1999):

Difference between slopes: $$(S_{xy}{}^{2})p = \frac{(residual\ SS)1 + (residual\ SS)2}{(residual\ DF)1 + (residual\ DF)2} \quad (8)$$

Where the subscripts 1 and 2 refer to the two regression lines being compared, SS refers to the sum of squares for each regression line, and DF refers to the degrees of freedom for each sample (Zar, 1999).